

A NEW SUBSPECIES OF *CLARKIA MILDREDIAE*
(ONAGRACEAE)

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ABSTRACT

Clarkia mildrediae subsp. *lutescens* is a newly described subspecies that is readily distinguished from subsp. *mildrediae* by the color of its anthers which may be bright yellow, yellow-orange, light orange or red-orange on different plants while those of subsp. *mildrediae* are magenta. Subspecies *lutescens* has a separate and nonoverlapping geographical distribution primarily in Butte and Plumas Counties where subsp. *mildrediae* is also found. Within subsp. *lutescens*, the proportion of plants with bright yellow anthers varies among populations from 98% to none. Bright yellow is homozygous and true breeding and is allelic to red-orange. Plants from populations with high proportions of bright yellow anthers also have shorter and narrower petals. Hybrids between the two subspecies are fully fertile.

Heller (1940) first distinguished *Clarkia mildrediae* (Heller) Lewis and Lewis as *Phaeostoma mildredae* from *P. atropurpureum* Heller, later included in the widespread *C. rhomboidea* Douglas (Lewis and Lewis 1955), on the basis of its larger flowers and later flowering. Lewis and Lewis (1955) determined that *P. mildredae* ($n = 7$) was one of the diploid parents of *C. rhomboidea* (the other being *C. virgata* Greene [$n = 5$]) and transferred it to *Clarkia* (Lewis and Lewis 1953). The relationship was proven by the finding (reported in Mosquin 1964) that experimental triploid hybrids between *C. mildrediae* and *C. rhomboidea* showed seven bivalents and five univalents at meiosis and those between *C. virgata* and *C. rhomboidea* showed five bivalents and seven univalents. The three species were recognized as *Clarkia* sect. *Myxocarpa* (Lewis and Lewis 1955). At that time, *C. mildrediae* was known only from a few localities on the North Fork of the Feather River in Butte and Plumas Counties and from the vicinity of Shasta Lake (Shasta County) to the north. Small (1971a, b) segregated the northern populations, by then extended to Trinity County, as *C. borealis* because of their virgate habit and lavender petals which differentiated them from *C. mildrediae* and because of the substantial differences between them in chromosomal arrangement which rendered their hybrids sterile. We

have been studying the species of sect. *Myxocarpa* (Gottlieb and Janeway 1995; Gottlieb and Ford unpublished) and our field work has led to the discovery of a new subspecies of *C. mildrediae* that we describe here as subsp. *lutescens*. The new subspecies has a separate and non-overlapping distribution, relative to subsp. *mildrediae*, in Butte and Plumas counties, and differs conspicuously in anther color and several other floral traits. Both subspecies are out-crossing and have the same chromosome number.

Anther color and genetics. Anthers of subsp. *mildrediae* are magenta and pollen is blue or blue-gray. Anthers of subsp. *lutescens* may be bright yellow, yellow-orange, light orange, or red-orange. Anther color is constant on each plant but may differ among plants within and between populations of subsp. *lutescens* (see below). In general, pollen color is correlated with anther color. Bright yellow anthers always have bright yellow pollen. Orange anthers are associated with tan or gray pollen, often with a yellow tinge, that sometimes darkens as the flower ages. Pollen of inner (epipetalous) anthers may initially appear yellow, darkening to tan, while pollen of the outer anthers may initially appear tan, darkening to a tan-gray, but never becoming blue or blue-gray. Anthers of subsp. *lutescens* are the same length as those of subsp. *mildrediae*, the outer ones generally 8–10 mm. They project forward of the four reddish-purple petals as in subsp. *mildrediae*, but their contrasting color, particularly when bright yellow, is an elegant and notable feature.

A preliminary genetic analysis of anther color has been carried out. Self-pollinated progeny of a plant grown from field-collected seed from subsp. *lutescens* population 4412 that had yellow-orange anthers and tan-yellow pollen showed bright yellow, yellow-orange, or orange anthers. Progeny with bright yellow and yellow-orange anthers were self-pollinated. Yellow-orange segregated progeny of three types: 13 bright yellow, 23 yellow-orange, and 12 orange anthers, suggesting that anther color in this cross was controlled by two alleles at a single locus and that the test plant was heterozygous. The progeny from plants with bright yellow anthers and pollen bred true, suggesting they were homozygous.

Experimental hybrids between subsp. *mildrediae* and subsp. *lutescens* have anthers and pollen of various colors depending on the allelic state of the controlling loci. To date, only a few crosses of this type have been grown. Magenta shows complete or incomplete dominance with orange and yellow in different crosses. The appearance of plants with magenta anthers and bright yellow pollen (a phenotype not observed in nature) in some progenies from inter-subspecific crosses suggests that the color differences between the subspecies are governed by at least two loci.

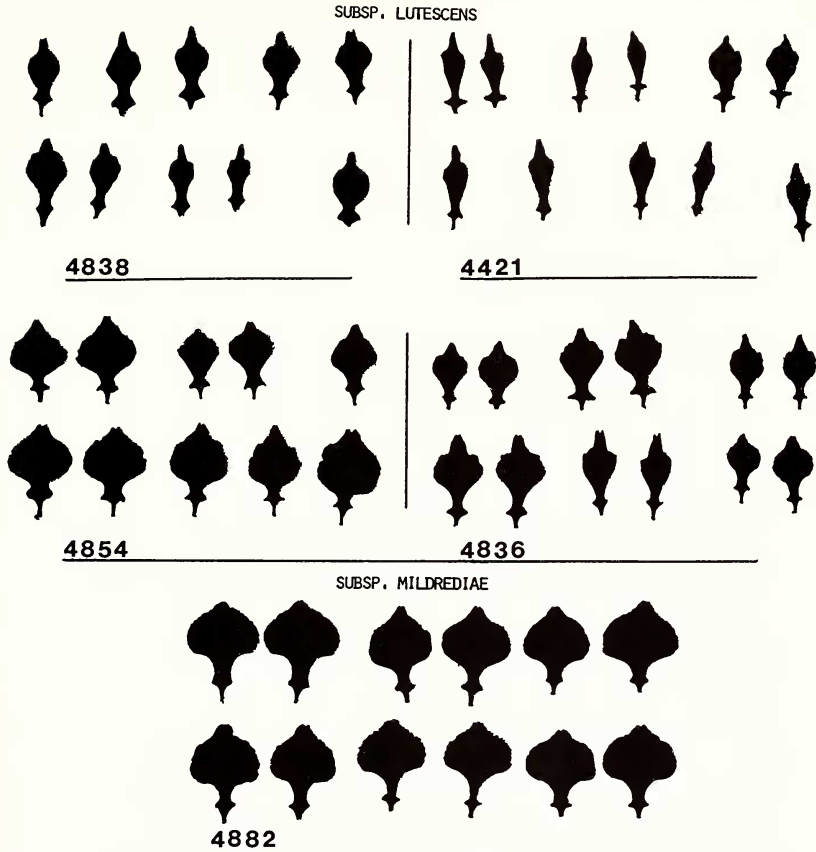


FIG. 1. Silhouettes of flower petals from representative populations of both subspecies of *C. mildrediae* grown in the greenhouse at Davis. For each plant, one petal was taken from both the first and second flower to open, on the day the stigma became receptive (usually three days after anthesis) because the petals are fully expanded then. The petals were placed on 3×5 cards under scotch tape which nicely preserves their size and shape. They were then xeroxed and the outlines filled in with black ink. Petals from five or six plants of each population are shown.

Petal shape. Petals of *C. mildrediae* have a deltoid or rounded limb that narrows into a claw with a pair of prominent lateral lobes above the slender base (Fig. 1). Petals from plants of numerous populations of both subspecies were measured in the field (Table 1) and also in the greenhouse (data not shown). Those of subsp. *mildrediae* are larger and broader. Within subsp. *lutescens*, plants from populations that have high proportions of light orange to red-orange anthers have nearly the same length and width as those of subsp. *mildrediae*. However, plants from populations that have predominantly bright yellow anthers and pollen, for example, populations

TABLE 1. PETAL LENGTH AND WIDTH COMPARISONS. Values reported (in mm) are means \pm 95% confidence limits for the population with the largest and the one with the smallest mean for each subspecies, with sample sizes in parentheses. Field measurements were of the second most recently opened flower which was generally one of the first three flowers on the inflorescence. The petals on each measured flower were fully expanded. Measurements were made in seven populations of *C. mildrediae* subsp. *mildrediae* and 13 of subsp. *lutescens*; sample sizes vary from 3 to 19 plants per population.

	subsp. <i>lutescens</i>		subsp. <i>mildrediae</i>	
Length	Pop. 4684	20.5 \pm 1.0 (10)	Pop. 4882	21.1 \pm 0.6 (14)
	Pop. 4837	16.1 \pm 0.6 (10)	Pop. 4681	18.8 \pm 0.7 (14)
	All pop.	17.8 \pm 0.3 (130)	All pop.	20.1 \pm 0.3 (88)
Width	Pop. 4693	14.9 \pm 1.4 (10)	Pop. 4882	16.7 \pm 0.8 (14)
	Pop. 4837	7.7 \pm 0.9 (10)	Pop. 4679	12.5 \pm 1.1 (8)
	All pop.	11.6 \pm 0.4 (130)	All pop.	14.9 \pm 0.5 (88)

4421 and 4839 (Table 2), have shorter and significantly narrower petals (Fig. 1). The basis of this correlation has not yet been studied.

Geographical distribution. *Clarkia mildrediae* is distributed nearly entirely within Butte and Plumas Counties, with a few outlying locations in adjacent Yuba and Sierra Counties, east of Sly Creek Reservoir (Fig. 2). The subspecies are entirely allopatric and have not been found growing intermixed at any locality. Subspecies *lutescens* occurs in openings in the Yellow Pine forest and adjacent habitats from the North Fork of the Feather River, south and east of Pulga, and east to Big Creek (east of Bucks Lake) and south across the drainage of the Middle and South Forks of the Feather River to Canyon Creek, a tributary of the North Yuba River. Subspecies *mildrediae* occurs along the North Fork of the Feather River south of Belden, and north and west to the West Branch of the Feather River in the vicinity of Stirling City. Overall, its distribution is northwest of that of subsp. *lutescens*. In two areas, near Pulga on the North

TABLE 2. PROPORTION OF PLANTS WITH BRIGHT YELLOW ANTERS AND POLLEN IN POPULATIONS OF *C. MILDREDIAE* SUBSP. *LUTESCENS*. Collections are those of LPJ.

Population	Number plants sampled	% bright yellow
4839	100	98
4421	50	98
4838	50	89
4429	41	34
4836	50	28
4854	108	3
4881	50	0
4687	40	0

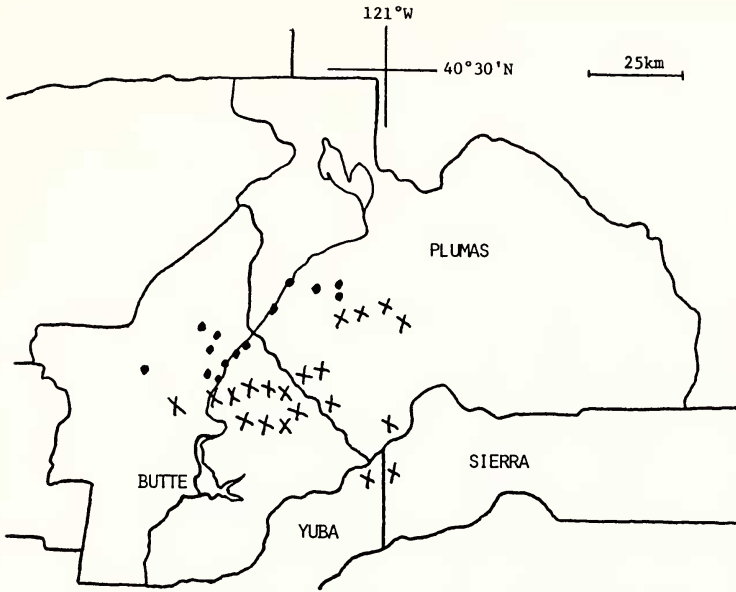


FIG. 2. Outline map of Butte, Plumas, and adjacent counties to show locations of collected populations of *C. mildrediae*. The North Fork of the Feather River is shown. Dots mark subsp. *mildrediae* and crosses mark subsp. *lutescens*.

Fork of the Feather River and southeast of Bucks Lake, populations of the two subspecies occur within several miles of each other.

In general, neither subspecies is known north or east of the vicinity of the Pacific Crest Trail in central Plumas County. Rainfall maps of the Plumas National Forest (Schultz and Benoit 1980) show that both subspecies are found in a region with mean annual precipitation greater than 145 cm; to the west and east of their distribution, the precipitation decreases rapidly. Both subspecies may be found in granitic, metamorphic or volcanic substrates and in elevations between 450 and 1700 meters.

As noted previously, populations of subsp. *lutescens* differ in the proportion of plants having different anther colors. Because bright yellow appears to be fully recessive to other colors and because this color can be readily identified, we scored the proportion of bright yellow in eight populations (Table 2). The proportion varied from 98% in populations 4421 and 4839 in the southwestern part of the distribution to zero or near zero in the northern and eastern portion. Populations that have predominantly bright yellow anthers seem to be restricted to Butte County.

Reproductive relationship. Pollen viability was examined in F_1 plants produced by crossing four pairs of populations representing

the two subspecies. The F_1 plants were vigorous and more than 98% of their pollen was stainable with acetocarmine and had a normal three-pored appearance. The plants set abundant seed after experimental pollination. Thus, the subspecies are fully interfertile and there is no evidence that they differ in chromosomal arrangement.

Conclusions. *Clarkia mildrediae* subsp. *lutescens* is readily distinguished from subsp. *mildrediae* by the color of its anthers and by the narrower petals in populations that have a high proportion of bright yellow anthers. Subspecies *lutescens* has a separate and non-overlapping geographical distribution in Butte and Plumas Counties where subsp. *mildrediae* is also found. The two have the same chromosome number and apparently the same chromosomal arrangement since their hybrids are fully fertile.

Subspecies *lutescens* was not recognized before now because previous students of *Clarkia* had not collected in its rugged territory. *Clarkia stellata* Mosquin, a predominantly self-fertilizing species that appears to have been derived from *C. mildrediae* (Mosquin 1962; Small 1971b) and is distributed in the same region of the northern Sierra Nevada, is probably derived from subsp. *lutescens* since both have yellow anthers and yellow pollen. We have designated the new taxon subsp. *lutescens* because the anthers, varying from bright yellow to red-orange on different plants, are its most distinctive feature.

TAXONOMY

Clarkia mildrediae (Heller) Lewis and Lewis subsp. ***lutescens*** Gottlieb and Janeway, subsp. nov.—TYPE: USA, California, Butte County, Plumas National Forest Road 28 at Chino Creek, 7 July 1995, *Janeway 4837* (Holotype, JEPS, Isotypes, CHSC, DAV, RSA).

A *C. mildrediae* (Heller) Lewis & Lewis subsp. *mildrediae* dif-
fert: antheris varians individuís luteis, flavis aurantiacis, aremeni-
acis, o rubris aurantiacis; petalorum limbo 7–16 mm lato.

Differs from *C. mildrediae* (Heller) Lewis & Lewis subsp. *mildrediae*: anthers of different individuals yellow, yellow-orange, orange-red, or red; petal limbs 7–16 mm wide.

Paratypes. USA, California, Butte County, on road crossing (Plumas N.F. Road 28) of Last Chance Creek, 28 July 1982, *Schlisling and Tarp 4358* (CHSC); along Bean Creek Road, ca. $\frac{3}{4}$ mi SW of Little Bald Rock, 29 June 1988, *Ahart 6102* (CAS, CHSC, MO); along French Creek Road 2.6 mi from Oroville-Quincy Hwy, 1 July 1993, *Janeway 4412* (CHSC, DAV); along French Creek Road 4.1 mi from Oroville-Quincy Hwy, 1 July 1993, *Janeway 4413* (CAS, CHSC); at the type locality Plumas N. F. Road 28 at Chino Creek,

2 July 1993, *Janeway 4421* (CAS, MO); 1.3 mi S-SW of Hungry Hunt Peak, 2 July 1993, *Janeway 4426* (CAS, CHSC); W end of Watson Ridge, 6 July 1993, *Janeway 4429* (CHSC, DAV); between Haphazard Creek and Baker and Foreman Creeks, 7 July 1994, *Janeway 4684* (CHSC); 1.3 mi S-SW of Hungry Hunt Peak, 7 July 1995, *Janeway 4836* (GH, MO, RSA, US); along French Creek Road 4.1 mi from Oroville-Quincy Hwy, 7 July 1995, *Janeway 4838* (LA, MO); between Mountain House, French Creek and Mosquito Creek, 7 July 1995, *Janeway 4839* (HSC, NY, RENO, US); Plumas County. Oroville-Quincy Hwy, 0.9 mi W of Grizzly Creek, 22 July 1993, *Janeway 4469* (CHSC, DAV); Hartman Bar Ridge, 8 July 1994, *Janeway 4687* (CHSC, DAV, JEPS, MO); between Lookout Rock and Middle Fork Feather River, 13 July 1994, *Janeway 4693* (CHSC, JEPS); Oroville-Quincy Hwy, 0.9 mi W of Grizzly Creek, 29 July 1995, *Janeway 4881* (CAS, MO, RSA, US); Sierra County. Rock Creek 0.3 mi NW of Canyon Creek, 1 July 1994, *Janeway 4676* (CHSC); Yuba County. Slate Creek, 3 mi NE of Strawberry Valley, 1 July 1994, *Janeway 4674* (CAS, CHSC); Slate Creek, 3 mi NE of Strawberry Valley, 15 July 1995, *Janeway 4854* (GH, MO, RSA, US).

Collection numbers and localities of the populations of subsp. *mildrediae* cited in the text are identified below (all collections are those of Janeway): *4679*: 0.7 mi E-SE of Flea Mountain (CHSC); *4681*: Granite Ridge, along the Concow Road (CHSC); *4720*: ¼ mi W of Bear Ranch Creek Falls in North Fork Feather River Canyon; *4858*: 0.8 mi NW of Oak Point (E of Stirling City) (CHSC, GH, NY, US); *4882*: Pipeline Road, NW of Bucks Lake (CHSC, DAV, JEPS, RSA).

ACKNOWLEDGMENTS

We thank Kent Holsinger for assistance with the Latin diagnosis, and the curators of the following herbaria for loans of specimens and access to their collections: CAS, CHSC, DS, GH, JEPS, HSC, LA, MO, NY, OSC, POM, RENO, RSA, UC, US. This study was supported in part by the Plumas National Forest (LPJ) and by National Science Foundation grant BSR 91-06831 (LDG).

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